

The first discovery of non-avian dinosaur egg clutch (*Macroolithus yaotunensis*, Elongatoolithidae) from the Upper Cretaceous Qiupa Formation of Tantou Basin

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Abstract The Upper Cretaceous of Tantou Basin in western Henan has yielded many vertebrate fossils, which are featured by several non-avian dinosaurs. Meanwhile, studies on their eggs were yet inadequate though many eggshells have been reported. The newly discovered material 41HV0199 was excavated from the Upper Cretaceous Qiupa Formation in 2021. The block preserves eight complete eggs arranged in two partial rings that form a partial clutch, and there are some scattered eggshells preserved closely with the block, showing a concave-up to concave-down ratio of 54.5:45.5, which indicates that the scattered eggshells come from the clutch and the clutch had been partially broken before it was buried. Based on morphological and microstructural characteristics, the eggs and eggshells can be assigned to *Macroolithus yaotunensis* (Elongatoolithidae), an oospecies known to be related to oviraptorids, which leads *Yulong mini* to be its probable producer. Besides, some eggshells show microstructural signs indicating egg retention, which marks the second example of egg retention in the oofamily Elongatoolithidae.

Key words Tantou Basin, Upper Cretaceous, Qiupa Formation, Dinosaur egg, *Macroolithus*

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1 Introduction

The western region of Henan Province has developed many Mesozoic-Cenozoic basins where many vertebrate fossils have been discovered. Among them, the Late Cretaceous fauna

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in the Tantou Basin of the Luanchuan area is featured by many non-avian dinosaurs as well as squamates, chelonians, mammals (Wei et al., 2021), and avians (Xu et al., 2021). The non-avian dinosaurs in Tantou Basin are very diverse, in which theropods are most numerous in species, including *Luanchuanraptor henanensis* (Lü et al., 2007), *Qiupalong henanensis* (Xu et al., 2011), *Yulong mini* (Lü et al., 2013), *Qiupanykus zhang*i (Lü et al., 2018) and *Tarbosaurus bataar* (Holtz, 2004) (= *Tyrannosaurus luanchuanensis*, Dong, 1979). There were also records of unnamed materials of ankylosaurs (Jia et al., 2010), ornithopods, and sauropods (Wei et al., 2021).

Related to the discovery of non-avian dinosaurs, there are abundant discoveries of non-avian dinosaur eggshells in the Tantou Basin. Zhou and Feng (2002) reported dinosaur eggshells in the Qiupa Formation. Liang et al. (2009) mentioned the occurrence of *Elongatoolithus* in the Qiupa Formation when reviewing the distribution of dinosaur eggs in Henan. Tanaka et al. (2011) described some eggshells from Qiupa Formation and stated that they are most similar to *Elongatoolithus* and *Macroolithus* of oofamily Elongatoolithidae without further determination, and they are usually thought to be produced by oviraptorids (Norell et al., 1994; Dong and Currie, 1996; Clark et al., 1999; Sato et al., 2005; Cheng et al., 2008; Weishampel et al., 2008). Therefore, the single eggshell preserved closely with the holotype of *Qiupanykus zhang*i was also interpreted to be produced by oviraptorids for its similarity with the elongatoolithid eggshells described by Tanaka et al. (2011), which supported that *Qiupanykus zhang*i may feed on oviraptorid eggs (Lü et al., 2018). Recently, Wei et al. (2021) reported a continuous collection of dinosaur eggshells from the Qiupa Formation. In contrast to the large number of eggshells, there is currently no discovery of a complete egg in the Tantou Basin.

In 2021, the joint field team of Henan Natural History Museum and the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences discovered an egg clutch during a field survey in Miaogou, Qiupa Town. In the same pit, the team also discovered some bones of mammals, squamates, and teeth of non-avian theropods. After careful excavation and preparation of the clutch, the eggshells were sampled for thin section preparation and identification. This specimen represents the first egg clutch and complete eggs discovered in the Upper Cretaceous Qiupa Formation of Tantou Basin. This work is a brief description of this clutch.

Institution abbreviation DM, Darwin Fossil Museum, Keelung, Taiwan, China; HNM, Henan Natural History Museum (= HGM, Henan Geological Museum), Zhengzhou, Henan, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LDNHMF, Lande Museum of Natural History, Tangshan, Hebei, China; NMNS, National Museum of Natural Science, Taichung, Taiwan, China; PFMM, Paleowonders Fossils and Mineral Museum, New Taipei, Taiwan, China.

2 Geological setting

Tantou Basin (Fig. 1) is a Mesozoic-Cenozoic basin located at the south of Xionger Mountain in Henan, which is about 80 km north of Luanchuan County, Luoyang. It belongs to the south edge of the North China Plate and nears the Qinling orogenic belt (Mao et al., 2012). The Upper Cretaceous to Paleogene red terrestrial strata in the Tantou Basin can be divided into Upper Cretaceous Qiupa Formation, Paleocene Gaoyugou Formation, Paleocene Dazhang Formation, and Eocene Tantou Formation in ascending order (Henan Provincial Bureau of Geology and Mineral Resources, 1989; Wei et al., 2021).

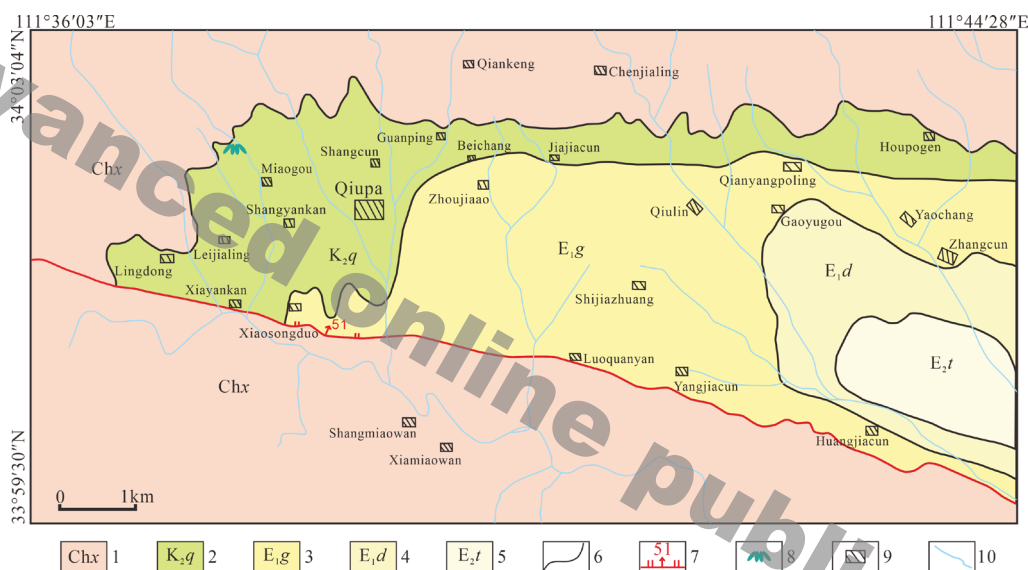


Fig. 1 Geological map of the west part of Tantou Basin (modified from Wei et al., 2021)

1. Xionger Group; 2. Qiupa Formation; 3. Gaoyugou Formation; 4. Dazhang Formation;
5. Tantou Formation; 6. Geological boundary; 7. Normal fault and its dip angle;
8. Excavation site of 41HV0199; 9. Settlement; 10. River system

3 Material and method

The materials include a block preserving eight nearly complete eggs that constitute an incomplete clutch and at least 22 in-situ eggshells (41HV0199) (Fig. 2A). The specimen was collected from the Upper Cretaceous Qiupa Formation from Miaogou, Yankan Village, Qiupa Town, Luanchuan County, Luoyang City, Henan Province, China. Numerous scattered eggshells were also collected from the same excavation site. The specimens are housed in Henan Natural History Museum (HNM).

Samples for thin-section preparation include in-situ eggshells from the clutch and scattered eggshells from the same site. Thin sections were prepared at the hard tissue thin section lab of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese

Academy of Sciences (IVPP). The eggshells were mounted with EXAKT Technovit 7200 resin before being cut with EXAKT 300CP automatic cutting machine and EXAKT 400CP speed-variable polisher to finally obtain thin sections that are about 30 μm in thickness. The thin sections were then observed and photographed with a Zeiss Axio imager A2m polarized microscope.

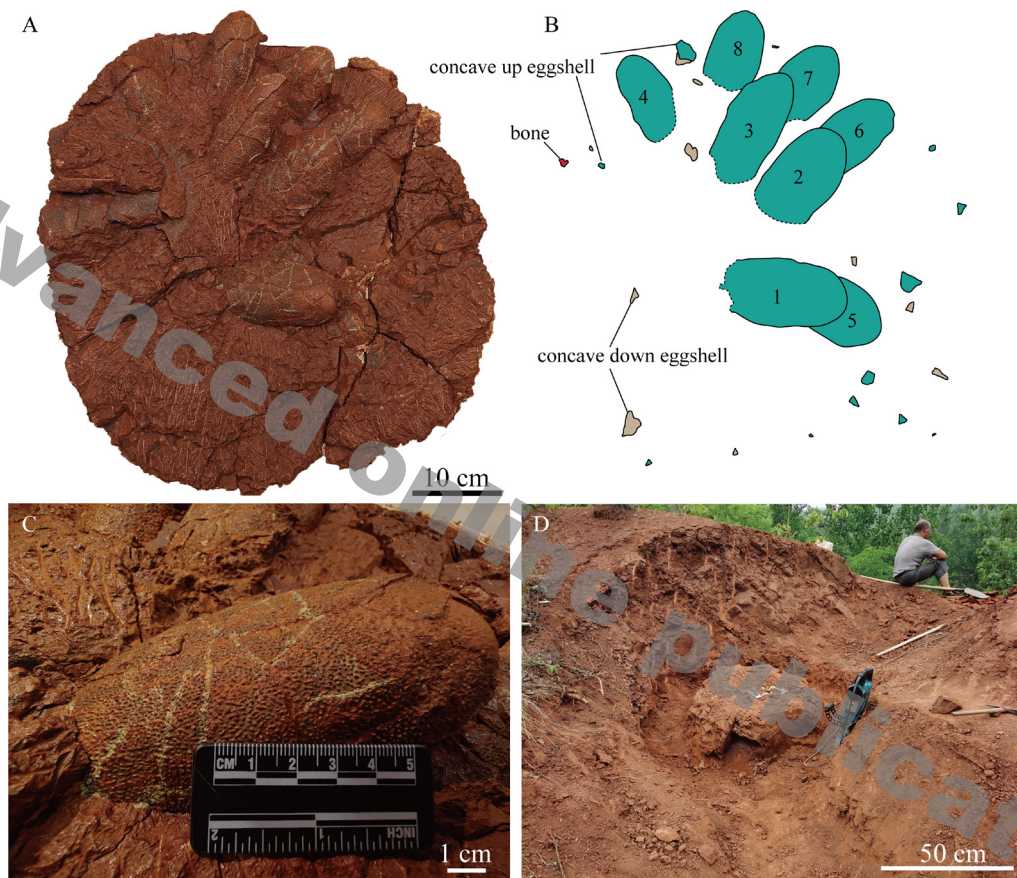


Fig. 2 41HV0199, a clutch of new *Macroolithus yaotunensis* material from Miaogou, Qiupa Town
 A. block containing the clutch, prepared from the bottom; B. sketch of A, showing eight remaining eggs (Ring 1: No. 1 to 4; Ring 2: No. 5 to 8) and 22 scattered in-situ eggshells, plus an unidentified bone fragment
 Note that those concave-up eggshells now have their outer surface towards our view;
 C. close view of egg No. 1, showing nodular surface resembles dispersituberculate ornamentation;
 D. photo of the original block containing the clutch (center) during the field excavation

4 Result

4.1 Taphonomy

During excavation, many fragmented eggshells were collected, all of which have very sharp edges and show no evidence of strong erosion, suggesting deposition near the origin though their orientation information was lost during excavation.

The carefully prepared block contains not only the clutch but also some in-situ eggshell fragments. There are twelve concave-up eggshells and ten concave-down eggshells in the block (ratio 54.5:45.5), which exceeds 50:50 and is typical of a colony (Hayward et al., 2000; Imai et al., 2015).

Since there is no other clutch nearby, we assume that all 22 in-situ eggshells from the clutch block and other scattered eggshells collected during excavation are most probably from the same clutch.

4.2 Systematic paleontology

Elongatoolithidae Zhao, 1975

***Macroolithus* Zhao, 1975**

***Macroolithus yaotunensis* Zhao, 1975**

Referred specimen 41HV0199, a clutch containing eight eggs and at least 22 in-situ eggshell fragments (Fig. 2A, B) as well as hundreds of scattered eggshell fragments collected from the excavation site.

Location and horizon Miaogou, Yankan Village, Qiupa Town, Luanchuan County, Luoyang City, Henan Province, China. Qiupa Formation, Upper Cretaceous.

Description Clutch structure The clutch was prepared from the bottom (Fig. 2A). Eight eggs that are nearly complete were arranged in two radiating rings that are both incomplete. The first ring has four eggs which include two eggs that form a pair and two eggs that are both isolated. The second ring also has four eggs which include two eggs that form a pair and two isolated eggs. The second ring has a larger diameter than the first ring. No trace of a third ring can be observed. Based on the arrangement and orientation of the eggs, all eight remaining eggs belong to the same half-side of the clutch. The estimated diameter of the complete clutch is about 45 cm, and the vacant center of the first ring has an estimated diameter of about 10 cm, which is not fully exposed.

Egg morphology None of the eight eggs is fully exposed since the internal ends of all eggs are still buried in the rock. Based on the partially exposed egg body, the full length of the eggs is estimated to be 17.0 to 18.5 cm, and the equatorial diameter is 8.0 to 8.5 cm, which might be slightly larger than the actual due to compression. The shape index ($100 \times \text{equatorial diameter} / \text{full length}$) is about 46.

Ornamentation The exposed part of the eight in-situ eggs is mostly decorated by small nodes (Fig. 2C), which resembles dispersituberculate ornamentation. The scattered eggshells show higher ornamentation diversity including dispersituberculate, ramotuberculate, and linearituberculate type (Fig. 3).

General microstructure The two eggshells from the clutch have a thickness that ranges from 0.84 to 1.07 mm without ornamentation and 0.95 to 1.29 mm when including, and the

scattered eggshell fragments surrounding the clutch are thicker and show larger range of 1.01 to 1.54 mm without ornamentation and 1.21 to 1.85 with ornamentation. The eggshell can be divided into two structural layers, which are the mammillary layer and the continuous layer (Fig. 4B). The two structural layers are separated by an abrupt and distinct boundary that is undulating.

Mammillary layer The mammillary layer is composed of a layer of closely arranged mammillae (Fig. 4B). The thickness varies due to its undulating upper boundary, which ranges from 0.12 to 0.33 mm from the samples taken from the clutch and 0.19 mm to 0.57 mm from the scattered eggshell fragments. The mammillae are wedge-shaped.

Continuous layer The continuous layer shows irregular mosaic extinction in most regions (Fig. 4B). In some scattered eggshells, there is occasionally a dark line that is close and parallel to the outer surface (Fig. 4D), causing discontinuity of grain extinction (Fig. 4E), which is abnormal and does not have diagnostic significance.

Pore system The pore system is of angusticanalicate type. The straight pore canals are



Fig. 3 Scattered eggshells around the clutch showing variation of ornamentation and microstructure from Miaogou, Qiupa Town

A. dispersituberculate; B. ramotuberculate; C. linearituberculate, ridge shaped;
D. linearituberculate, chain shaped

perpendicular to the outer surface and unbranched (Fig. 4A). On the tangential section through the middle part of the eggshell, the pore canals are round to oval in shape (Fig. 4C), and the diameter is 75 to 85 μm .

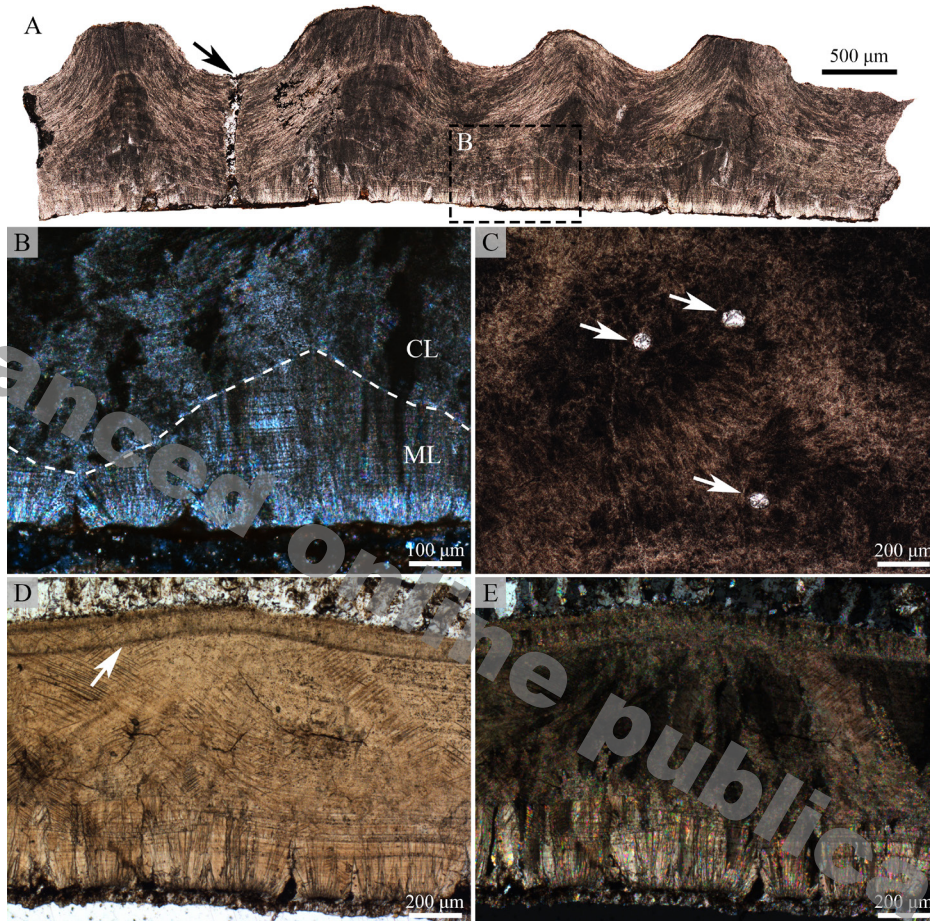


Fig. 4 Microstructure of 41HV0199 from Miaogou, Qiupa Town

A–C. an eggshell from the equatorial region of egg No. 6 (Fig. 2B): A. radial view, showing undulating outer surface and a straight pore canal (black arrow); B. enlargement near the inner surface, polarized light, showing undulating and abrupt boundary between the mammillary layer (ML) and continuous layer (CL) The wedge shaped mammillae are closely arranged and the continuous layer shows irregular extinction;

C. tangential view of the continuous layer, showing round to oval pore canals (white arrows)

D, E. a scattered eggshell with abnormal structure: D. radial view of the eggshell, showing a black line (white arrow) near the outer surface; E. polarized light view of D, showing distinct change of extinction pattern after passing the dark line

5 Discussion

5.1 Origin of the scattered eggshells

The taphonomy analysis supports the origin of the scattered eggshells from the clutch 41HV0199, although there are still some differences that need to be discussed. The general

microstructure of the scattered eggshells is basically the same as those sampled from the clutch, but some of them show linearituberculate ornamentation. Besides, the scattered eggshells are generally thicker. These differences can be simply explained by the small sample size ($n = 2$) of eggshells taken from the clutch and the thickness variation caused by the position difference on the egg body, as the eggshell thickness can vary a lot even for eggshells from the same egg. Take *Elongatoolithus frustrabilis* (Elongatoolithidae) for example, eggshells from the blunt end of the egg can reach 1.1 to 1.2 mm in thickness while those from the equatorial region are only 0.5 to 0.6 mm (Mikhailov, 1997).

5.2 Comparison

The structure morphotype of 41HV0199 is typical of the ratite morphotype. The features of the elongated body, two structure layers, and dispersituberculate ornamentation that is slightly orientated in the equatorial region resemble the oofamily Elongatoolithidae and Macroelongatoolithidae. Macroelongatoolithidae usually have a length larger than 40 cm, while Elongatoolithidae usually have eggs that are 10 to 20 cm in length. In consequence, 41HV0199 can be assigned to Elongatoolithidae.

After the latest revision (Zhu et al., 2024), there are currently 6 oogenera left in Elongatoolithidae, including *Elongatoolithus*, *Macroolithus*, *Nanhsiungoolithus*, *Undulatoolithus*, *Trachoolithus*, *Ellipsoolithus*. Besides, two North American oogenera are also similar to members of Elongatoolithidae (Zhao et al., 2015), so we also compared them with 41HV0199.

Compared with 41HV0199, eggs of *Elongatoolithus* usually have smaller egg body (length ranges 11 to 17 cm, equatorial diameter ranges 5.8 to 8.2 cm) and thinner eggshell (0.30 to 1.50 mm) (Mikhailov, 1994; Zhao et al., 2015), the boundary of its mammillary layer and continuous layer is gradual rather than abrupt (Zhao, 1975). *Nanhsiungoolithus* has broad mammillae and a continuous layer that shows columnar extinction, and its ornamentation is not very prominent (Zhao, 1975; Zhu et al., 2024). *Undulatoolithus* and *Trachoolithus* have more elevated decoration (Wang et al., 2013; Zhu et al., 2024). The egg of *Ellipsoolithus* is smaller (length ranges 9.8 to 11 cm, equatorial diameter ranges 6.5 to 8 cm) in size and more oval in shape, and its equatorial region is decorated by short ridges (Mohabey, 1998).

Porituberoolithus has pore openings on top of the nodes, which is not seen on any members of Elongatoolithidae or 41HV0199, it also has a significantly thinner eggshell (0.5 to 0.65 mm). Zhu et al. (2024) argued that there is possibly an external zone in the continuous layer of *Continuoolithus*, which is similar to *Heishanoolithus*. *Heishanoolithus* was expelled from Elongatoolithidae due to the presence of an external zone that shows columnar extinction outside of the squamatic zone, which is not observed in 41HV0199, so 41HV0199 cannot be either *Continuoolithus* or *Heishanoolithus*.

Macroolithus has a similar egg length (17.6 to 20.8 cm) and slightly thicker eggshell

thickness (1.39 to 2.0 mm) compared to 41HV0199 (Table 1). The eggshell of *Macroolithus* also has an abrupt boundary between the mammillary and the continuous layer (Zhao, 1975), and has at least three extinction patterns in the continuous layer which can be observed in 41HV0199 (Zhu et al., 2024). In conclusion, 41HV0199 should be assigned to *Macroolithus*.

Macroolithus is one of the representative oogenus of Elongatoolithidae and a common member in the Late Cretaceous strata in Asia. Fragments of *Macroolithus* have been reported from the Late Cretaceous of North America (Jensen, 1970), which were later reassigned to *Macroelongatoolithus* (Simon et al., 2019). *M. turolensis* was once regarded as the sole representative of Elongatoolithidae in Europe (Amo Sanjuán et al., 2000), but was later revised to an oogenus *Guegoolithus* (Moreno-Azanza et al., 2014) that does not belong to Elongatoolithidae. As a result, there are currently three oospecies left in *Macroolithus*, which are *M. rugustus*, *M. yaotunensis*, and *M. mutabilis*. The thickness of *M. mutabilis* ranges from 1.3 to 2.0 mm (can exceed 2.3 mm with ornamentation), which is close to or slightly thicker than the other two oospecies and 41HV0199. However, no complete egg has been discovered for further comparison (Mikhailov, 1994). Compared to *M. rugustus* and *M. yaotunensis*, 41HV0199 has a comparable or slightly thinner eggshell and similar egg size. The eggshell of 41HV0199 has an undulating boundary between the mammillary and the continuous layers, which is the same as *M. yaotunensis* but contrary to the flat boundary in *M. rugustus*. Therefore, 41HV0199 could be assigned as a new specimen of *M. yaotunensis* based on its macro- and microstructure.

Table 1 Comparison between 41HV0199 and *Macroolithus* oospecies

Ootaxon/ Specimen	Length×equatorial diameter (cm)	Whole thickness (mm)	Mammillary layer thickness	Boundary between structure layers	Reference
<i>M. rugustus</i>	(16.5–18.1)× (7.5–8.5)	1.44–1.70	0.41	abrupt and flat	Zhao, 1975
<i>M. yaotunensis</i>	(17.6–20.8)× (6.7–9.4)	1.39–1.93	0.29–0.51	abrupt and undulating	Zhao, 1975
<i>M. mutabilis</i>	NA	1.3–2.0 (up to 2.3 with ornamentation)	NA	NA	Mikhailov, 1994
41HV0199	(17.0–18.5)× (8.0–8.5)	0.84–1.54 (0.95–1.85 with ornamentation)	0.12–0.57	abrupt and undulating	This work

5.3 Identification of egg retention in *Macroolithus*

The dark line occasionally observed in the continuous layer near the outer surface of some eggshells has not been described from any *Macroolithus* specimen before. However, this phenomenon resembles the boundary of a normal eggshell and an overlying abnormal structure in avians and turtles that is caused by egg retention (Ewert et al., 1984; Jackson and Varricchio, 2003; Jackson and Schmitt, 2008). We do not think this line represents a boundary between two structure layers or zones because boundaries between different structure layers or zones usually do not appear in a clear dark line under transmitted light microscope. Multilayered eggshells or additional abnormal layers can occur if the egg stays longer than expected, which

can also happen in dinosaur eggshells (Zelenitsky and Hills, 1997; Jackson et al., 2004; Grellet-Tinner et al., 2010). Recently, the first example of structure caused by egg retention in members of Elongatoolithidae has been reported in *Undulatoolithus* (Zhu et al., 2024). Similar to that in *Undulatoolithus*, the abnormal layer in *Macroolithus* does not form a complete layer of eggshell.

5.4 Clutch structure and possible producer

The oospecies *Macroolithus yaotunensis* can be safely related to oviraptorids by many cases of in-ovo embryos or eggs (sometimes even clutches) associated with skeletons (Sato et al., 2005; Cheng et al., 2008; Wang et al., 2016; Jin et al., 2020; Bi et al., 2021), which are all from the Upper Cretaceous of Ganzhou, Jiangxi Province, China.

The unique clutch structure of *M. yaotunensis* has been reconstructed by former researchers (Yang et al., 2019). Like other elongatoolithid clutches, the eggs are regularly arranged within the clutch. The eggs are paired and radially arranged into one to four concentric rings with successively increasing radii. The eggs are tilted while the blunt ends are higher and oriented toward the center. The 41HV0199 clutch shows eight remaining eggs arranged in two rings. The first ring is incomplete because the first ring of *M. rugustus* usually has eight to twelve eggs when complete (Yang et al., 2019). However, there are already four eggs in the second ring of 41HV0199, so the incompleteness of the first ring was not caused by the leave of the producer and may have ten eggs in its original state. The four eggs in the second ring are all arranged just above the four eggs of the first ring, and would have about 16 eggs if the second ring was fully completed. The remaining eight eggs of 41HV0199 come from the same half side of the clutch. It can be easily inferred that the clutch was partly broken before it was buried. It is not sure if there was a third ring in 41HV0199 because there is no supporting evidence.

If there were no third rings in the clutch 41HV0199, then the diameter of 41HV0199 is about 45 cm if the remaining two rings are both complete, which is slightly smaller than all reported *Macroolithus* clutches (Table 2). Many *Macroolithus* clutches have three rings, so it is reasonable that they are larger than 41HV0199 in size, however, clutches with only two rings are still larger than 41HV0199. Such differences may be caused by compression, or the smaller diameter of the vacant center, but more probably by the different body sizes of its producers. It would be natural to assume that the dinosaur producing 41HV0199 may be smaller than the one reported by Bi et al. (2021), which weighs about 110 kg (Hogan, 2024). The egg length of 41HV0199 is also shorter than that of LDNHMF2008, which also supports the presumption.

The only oviraptorid dinosaur reported in Tantou Basin is a derived member of Oviraptorosauria, *Yulong mini*, which includes at least five baby individuals of similar age that were less than one year old (Lü et al., 2013). However, these individuals are too young and small. Recently, a sub-adult specimen of *Yulong mini* that is about five or six years old

was found only a few hundred meters away from the excavation site of the clutch 41HV0199, which was also associated with a piece of elongatoolithid eggshell (Wei et al., 2022). The egg length of 41HV0199 is comparable with the *Macroolithus yaotunensis* egg pair reported in the body cavity of a female oviraptorosaurian dinosaur (NMNS-VPDINO-2002-0901) (Sato et al., 2005). The first two caudal vertebrae remaining in NMNS-VPDINO-2002-0901 are 3.8 to 4.3 cm in length, and the caudal vertebrae in the mid-proximal portion of the whole tail are 3.7 to 3.9 cm in length, which are also generally comparable (measured from figures). Another similar association of *M. yaotunensis* and oviraptorid dinosaur (Jin et al., 2020) has eggs that are slightly longer (about 19 cm) and shorter proximal caudal vertebrae (about 2.6 to 3 cm), and the individual is somatically premature while already sexually mature. Therefore, the body size of *Yulong mini* is suitable for giving birth to clutch 41HV0199, allowing it to be a probable producer of the eggs.

Table 2 Clutch comparison between 41HV0199 and other *Macroolithus* clutches

Ootaxon	Specimen No.	Diameter (cm)*	Number of rings	Clutch size	References
<i>M. rugustus</i>	IVPP V 2788	53.4	3	18 (6+10+2)	Zhao, 1975
<i>M. oosp.</i>	41HV0074 (HNM)	69.5	2–3	30 (12+16+2)	Yang et al., 2019
<i>M. oosp.</i>	DM-2014-P0154	~65.6	4	31 (8+13+7+?)	Yang et al., 2019
<i>M. oosp.</i>	PFMM-0014002972	65.4	3	32 (10+16+6)	Yang et al., 2019
<i>M. oosp.</i>	PFMM-0014004392	73.5	3	32 (10+18+4)	Yang et al., 2019
<i>M. oosp.</i>	PFMM-0014003019	68.7	3	35 (10+18+7)	Yang et al., 2019
<i>M. yaotunensis</i>	IVPP V 2784	71	2	20 (8+12)	Zhao, 1975
<i>M. yaotunensis</i>	LDNHMF2008	87.55	3	24 (3+9+12) incomplete	Bi et al., 2021; Hogan, 2024
<i>M. yaotunensis</i>	41HV0199 (HNM)	45	2	8 preserved, 26 (10+16) predicted	This work

Note: * Some data of the clutch diameter was estimated by measurements from the original pictures if the data was not given in the literature.

6 Conclusion

The newly discovered clutch 41HV0199 from the Upper Cretaceous Qiupa Formation in Tantou Basin can be assigned to *Macroolithus yaotunensis* (Elongatoolithidae). This discovery represents the first report of complete non-avian dinosaur eggs and a partial clutch in this area. The new material represents the smallest *Macroolithus* clutch and is most likely been produced by oviraptorosaurian dinosaurs in the basin, probably *Yulong mini*.

Egg retention in eggshells of *M. yaotunensis* was recognized for the first time, which represents the second member of Elongatoolithidae with a record of egg retention.

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潭头盆地上白垩统秋扒组首次发现非鸟恐龙蛋窝 (瑶屯巨形蛋, 长形蛋科)

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摘要: 豫西潭头盆地上白垩统中已发现了多种脊椎动物化石, 以数种非鸟恐龙类的发现为特点。盆地内也同时报道有大量的蛋壳, 然而关于这些蛋壳的研究却还不足。新材料 41HV0199 为 2021 年发掘自潭头盆地上白垩统秋扒组。岩石中保存了 8 枚完整蛋体, 组成一不到一半的部分蛋窝, 此外还保存有若干分散于围岩中的破碎蛋壳, 其凹面向上与凹面向下者的比例为 54.5 : 45.5, 指示这些蛋壳可能直接来源于该蛋窝, 且蛋窝在埋藏前发生了部分破碎。基于宏观形态与显微结构的特征, 这些蛋和蛋壳可被归入长形蛋科的瑶屯巨形蛋 (*Macroolithus yaotunensis*)。该蛋种已知与窃蛋龙类直接相关, 而盆地内发现的迷你豫龙 (*Yulong mini*) 可能是该蛋窝的产蛋者。此外, 在个别蛋壳中还发现了指示蛋体滞留的显微结构, 这是此类病态结构在长形蛋科中的第二例发现。

关键词: 潭头盆地, 上白垩统, 秋扒组, 恐龙蛋, 巨形蛋属

References

- Amo Sanjuán O, Canudo J I, Cuenca-Bescós G, 2000. First record of elongatoolithid eggshells from the Lower Barremian (Lower Cretaceous) of Europe (Cuesta Corrales 2, Galve Basin, Spain). In: Bravo A M, Reyes T eds. First International Symposium on Dinosaur Eggs and Babies Extended Abstracts. Isona i Conca Dellà. 7–14
- Bi S D, Amiot R, Peyre de Fabrègues C et al., 2021. An oviraptorid preserved atop an embryo-bearing egg clutch sheds light on the reproductive biology of non-avian theropod dinosaurs. *Sci Bull*, 66: 947–954
- Cheng Y N, Ji Q, Wu X C et al., 2008. Oviraptorosaurian eggs (Dinosauria) with embryonic skeletons discovered for the first time in China. *Acta Geol Sin - Engl*, 82: 1089–1094
- Clark J M, Norell M A, Chiappe L M, 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *Am Mus Novit*, 3265: 1–36
- Dong Z M, 1979. Dinosaur fossils from the Cretaceous of southern China. In: Institute of Vertebrate Paleontology and Paleoanthropology, Nanjing Institute of Geology and Paleontology eds. *Mesozoic and Cenozoic Red Beds in Southern China*. Beijing: Science Press. 342–350

- Dong Z M, Currie P J, 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Can J Earth Sci*, 33: 631–636
- Ewert M A, Firth S J, Nelson C E, 1984. Normal and multiple eggshells in batagurine turtles and their implications for dinosaurs and other reptiles. *Can J Zool*, 62: 1834–1841
- Grellet-Tinner G, Corsetti F, Buscalioni A D, 2010. The importance of microscopic examinations of eggshells: Discrimination of bioalteration and diagenetic overprints from biological features. *J Iber Geol*, 36: 181–192
- Hayward J L, Zelenitsky D K, Smith D L et al., 2000. Eggshell taphonomy at modern gull colonies and a dinosaur clutch site. *Palaios*, 15: 343–355
- Henan Provincial Bureau of Geology and Mineral Resources, 1989. Regional Geology of Henan Province. Beijing: Geological Press. 1–722
- Hogan J D, 2024. The egg-thief architect: experimental oviraptorosaur nesting physiology, the possibility of adult-mediated incubation, and the feasibility of indirect contact incubation. *Paleobiology*, 50: 108–122
- Holtz T R, 2004. Tyrannosauroida. In: Weishampel D B, Osmólska H, Dodson P eds. *Dinosauria II*. Berkeley: University of California. 111–136
- Imai T, Varricchio D J, Cahoon J et al., 2015. Sedimentological analyses of eggshell transport and deposition: implication and application to eggshell taphonomy. *Palaios*, 30: 435–445
- Jackson F D, Varricchio D J, 2003. Abnormal, multilayered eggshell in birds: implications for dinosaur reproductive anatomy. *J Vert Paleont*, 23: 699–702
- Jackson F D, Schmitt J G, 2008. Recognition of vertebrate egg abnormalities in the Upper Cretaceous fossil record. *Cretac Res*, 29: 27–39
- Jackson F D, Garrido A, Schmitt J G et al., 2004. Abnormal, multilayered titanosaur (Dinosauria: Sauropoda) eggs from in situ clutches at the Auca Mahuevo locality, Neuquén Province, Argentina. *J Vert Paleont*, 24: 913–922
- Jensen J A, 1970. Fossil eggs in the Lower Cretaceous of Utah. *Brigh Young Univ Geol Stud*, 17: 51–65
- Jia S H, Lü J C, Xu L et al., 2010. Discovery and significance of ankylosaur specimens from the Late Cretaceous Qiupa Formation in Luanchuan, Henan, China. *Geol Bull China*, 29: 483–487
- Jin X S, Varricchio D J, Poust A W et al., 2020. An oviraptorosaur adult-egg association from the Cretaceous of Jiangxi Province, China. *J Vert Paleont*, 39: e1739060
- Liang X Q, Wen S N, Yang D S et al., 2009. Dinosaur eggs and dinosaur egg-bearing deposits (Upper Cretaceous) of Henan Province, China: Occurrences, palaeoenvironments, taphonomy and preservation. *Prog Nat Sci*, 19: 1587–1601
- Lü J C, Xu L, Zhang X et al., 2007. New dromaeosaurid dinosaur from the Late Cretaceous Qiupa Formation of Luanchuan area, western Henan, China. *Geol Bull China*, 26: 777–786
- Lü J C, Currie P J, Xu L et al., 2013. Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications. *Naturwissenschaften*, 100: 165–175
- Lü J C, Xu L, Chang H L et al., 2018. A new alvarezsaurid dinosaur from the Late Cretaceous Qiupa Formation of Luanchuan, Henan Province, central China. *China Geol*, 1: 28–35
- Mao Z F, Zhou H R, Li S J et al., 2012. Palaeoclimates in the Tantou Basin, Luanchuan, western Henan during the Cretaceous-Palaeogene. *Sedi Geol & Teth Geol*, 33: 18–24
- Mikhailov K E, 1994. Theropod and protoceratopsian dinosaur eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontol J*, 28: 101–120

- Mikhailov K E, 1997. Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Spec Pap Palaeontol*, 56: 1–80
- Mohabey D M, 1998. Systematics of Indian Upper Cretaceous dinosaur and chelonian eggshells. *J Vert Paleont*, 18: 348–362
- Moreno-Azanza M, Canudo J I, Gasca J M, 2014. Spheroolithid eggshells in the Lower Cretaceous of Europe. Implications for eggshell evolution in ornithischian dinosaurs. *Cretac Res*, 51: 75–87
- Norell M A, Clark J M, Demberelyin D et al., 1994. A theropod dinosaur embryo and the affinities of the flaming cliffs dinosaur eggs. *Science*, 266: 779–782
- Sato T, Cheng Y N, Wu X C et al., 2005. A pair of shelled eggs inside a female dinosaur. *Science*, 308: 375–375
- Simon D J, Varricchio D J, Jin X S et al., 2019. Microstructural overlap of *Macroelongatoolithus* eggs from Asia and North America expands the occurrence of colossal oviraptorosaurs. *J Vert Paleont*, 38: e1553046
- Tanaka K, Lü J C, Kobayashi Y et al., 2011. Description and phylogenetic position of dinosaur eggshells from the Luanchuan area of western Henan Province, China. *Acta Geol Sin - Engl*, 85: 66–74
- Wang Q, Zhao Z K, Wang X L et al., 2013. A new form of Elongatoolithidae, *Undulatoolithus pengi* oogen. et oosp. nov. from Pingxiang, Jiangxi, China. *Zootaxa*, 3746: 194–200
- Wang S, Zhang S K, Sullivan C et al., 2016. Elongatoolithid eggs containing oviraptorid (Theropoda, Oviraptorosauria) embryos from the Upper Cretaceous of Southern China. *BMC Evol Biol*, 16: 67
- Wei X F, Kundrát M, Xu L et al., 2022. A new subadult specimen of oviraptorid *Yulong mini* (Theropoda: Oviraptorosauria) from the Upper Cretaceous Qiupa Formation of Luanchuan, central China. *Cretac Res*, 138: 105261
- Wei X F, Xia M L, Xu L et al., 2021. Advances of the studies on Late Cretaceous vertebrate fauna from Luanchuan in Henan Province. *Geol Bull China*, 40: 1178–1188
- Weishampel D B, Fastovsky D E, Watabe M et al., 2008. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *J Vert Paleont*, 28: 1110–1119
- Xu L, Buffetaut E, O'Connor J K et al., 2021. A new, remarkably preserved, enantiornithine bird from the Upper Cretaceous Qiupa Formation of Henan (central China) and convergent evolution between enantiornithines and modern birds. *Geol Mag*, 158: 2087–2094
- Xu L, Kobayashi Y, Lü J C et al., 2011. A new ornithomimid dinosaur with North American affinities from the Late Cretaceous Qiupa Formation in Henan Province of China. *Cretac Res*, 32: 213–222
- Yang T R, Wiemann J, Xu L et al., 2019. Reconstruction of oviraptorid clutches illuminates their unique nesting biology. *Acta Palaeontol Pol*, 64: 581–596
- Zelenitsky D K, Hills L V, 1997. Normal and pathological eggshells of *Spheroolithus albertensis*, oosp. nov., from the Oldman Formation (Judith River Group, Late Campanian), southern Alberta. *J Vert Paleont*, 17: 167–171
- Zhao Z K, 1975. The microstructure of fossil dinosaur eggs from Nanxiong County, Guangdong Province: concurrent with a discussion on the problem of the classification of dinosaur eggs. *Vert PalAsiat*, 13: 105–117
- Zhao Z K, Wang Q, Zhang S, 2015. Dinosaur eggs. Beijing: Science Press. 1–163
- Zhou S Q, Feng Z J, 2002. Studies on the occurrence beds of oöolithus and their relations to the upper-lower boundaries in Henan Province. *Res Surv Environ*, 23: 68–76
- Zhu X F, Wang Q, Wang X L, 2024. Electron backscatter diffraction (EBSD) study of elongatoolithid eggs from China with microstructural and parataxonomic implications. *Paleobiology*, 50: 330–345